Out of the Swamps

How early vertebrates established a foothold—with all 10 toes—on land

By RICHARD MONASTERSKY

Roughly 340 million years ago, a small beast built somewhat like a lizard was scampering along the edge of a tropical lagoon when it met its fate. No one knows what killed the wiener-size creature. A tropical storm might have drowned it, or perhaps a sudden wave washed it from shore. In any event, the animal fell into the lagoon and sank into the annals of paleontology.

In 1992, an amateur fossil collector spotted the remnants of this four-legged creature on the shore of Cheese Bay, Scotland. For the next 5 years, the fossil sat in a drawer at the National Museums of Scotland in Edinburgh, where researchers were engrossed in ongoing projects. Finally, paleontologists retrieved the headless specimen and started the painstaking process of chipping away the rock.

"We knew it was there in the drawer, but I don't think any of us recognized how interesting it was," says Tim R. Smithson of Cambridge Regional College in England.

Their indifference quickly faded. As Smithson and his colleagues watched the fossil emerge from the rock, they discovered signs that this creature had lived on land, making it the earliest known animal with a backbone to conquer the continents. They dubbed it *Casineria*, taking the name from the Latin words for cheese and bay.

With its four strong limbs and dexterous fingers, *Casineria* opened a new, drier chapter in humanity's deep prehistory, Smithson and his colleagues argue in the April 8 NATURE. Before this animal's time, the early Carboniferous period, vertebrates had spent more than 160 million years underwater, with only the most fleeting forays onto the land. *Casineria* and its kin, for the first time, sported a set of traits that freed them from the confines of the oceans and allowed them to make a living in some of the earliest forests on the planet, say the researchers.

The Cheese Bay find caps a decade of discovery during which paleontologists have uncovered several of the principal characters in the chronicle of early vertebrate evolution. Taken together, the fossils are starting to illuminate the biological steps—both small and profound—that led our ancestors from the security of the watery world to the expansive opportunities available on the harsh, desiccated continents.

Acanthostega *lurked in shallow waters of coastal swamps.*

Before *Casineria* entered the story, the main events in vertebrate evolution had played out underwater. Fish, the first animals with backbones, had appeared by the early Ordovician period, some 500 million years ago, and they remained the only vertebrates until around 360 million years ago.

At that time, the end of the Devonian period, some new styles of creatures appeared on the scene. First came fish with two pairs of stout, fleshy fins—evolutionary forerunners of arms and legs. From these lobe-finned fish then arose the earliest members of the tetrapods, or vertebrates with four true limbs.

For most of this century, the best picture of Devonian tetrapods came from a fossil species discovered by Swedish scientists in Greenland in the 1930s. The animal, called *Ichthyostega,* seemed like a vertebrate version of a sport utility vehicle—built for traversing all sorts of terrain. The size of a desk, it had arms, legs, hands, and feet, apparently for walking on land, but it also had a fishlike tail that could have served the animal only in the water.

In the eyes of the Swedish paleontologists, *Ichthyostega* lived its life between two realms, half in and half out of water. Their studies of this creature suggested that the development of limbs coincided with the time that vertebrates first started crawling out on land, which made a certain amount of sense. After all, what good would hands and feet be on a fish?

In the late 1980s, a pair of scientists from the University of Cambridge in England came up against just that question. In an expedition to Greenland, Jennifer Clack discovered complete specimens of another Devonian tetrapod, called *Acanthostega.* Scientists had previously collected only scraps of it. When Clack and Michael I. Coates studied the full skeleton of *Acanthostega* in 1989, they found hands and feet attached to an essentially aquatic animal.

What's more, *Acanthostega*'s hands were some of the oddest known. Instead of having five digits—which was assumed to be the ancestral pattern among tetrapods—*Acanthostega* had an overabundance of fingers, eight on each hand. Flummoxed by this, Clack and Coates set upon a recently discovered leg of *Ichthyostega* to see what it was hiding at the end of its limbs. They found that *Ichthyostega* had seven toes on each foot rather than the five that the Swedish researchers had assumed.

Clack and Coates realized that *Acanthostega* and *Ichthyostega* could not have managed to do much more than flop around on land. Their upper arm bones, instead of being long and slender, had a broad, blobby shape ill-suited for walking. Their hind limbs splayed out to the side and could not have held up the body easily.

"If you look at their skeletal anatomy, they look very aquatic. The limbs are pretty much paddles. They've got fishlike tails. And we know from the skull that they have all sorts of adaptations for existing in an aquatic environment," says Coates, now at University College London.

So fingers, toes, and other elements of a vertebrate limb evolved before tetrapods spent any quality time on land. These skeletal novelties must have served some purpose in the shallow lagoons where *Ichthyostega* and *Acanthostega* lived, concluded Clack and Coates.

Fast forward 20 million years to the era of *Casineria*, which is the next time paleontologists get a good look at tetrapods.

"We've got the Devonian beasties and then there was a huge gap in the fossil record before we get any evidence of terrestriality or diversity of tetrapods. *Casineria* is beginning to fill that gap," says Clack, who collaborated with Smithson in studying the fossil.

Compared with the meter-long Devonian tetrapods, *Casineria* is a wee thing. The fossil is missing its head and tail, so paleontologists cannot definitively measure its length. Smithson estimates that the animal stretched only 15 centimeters from head to tail.

Looking in detail at the skeleton, the British researchers found a variety of adaptations to terrestrial life. *Casineria*'s vertebrae, for example, connected to each other to form a relatively stiff backbone, which would have served as a suspension bridge to hold up the animal's body. The Devonian tetrapods, by contrast, had much looser backbones that are similar to those of fish, which offer less support, says Smithson.

The upper arm bone, or humerus, of *Casineria* had a shaft in the middle and flared out on each end—the kind of shape that a dog could get its mouth around. The squat humerus of *Acanthostega*, however, would have baffled a poor dog because it didn't narrow at its middle.

Casineria's proportionately longer, more slender design would have held the animal up better and helped while it walked. "The humerus is much more like that of primitive reptiles than it is like that of primitive tetrapods," says Smithson.

The advances continue all the way down to the end of the limbs, where *Casineria* has a neat set of five digits on each hand and foot—establishing the fundamental pattern that runs through the rest of vertebrate evolution, even to the tips of our fingers. Some animals, such as horses, have lost several digits through time, but no land vertebrate has evolved a hand with more than five true digits.

When Smithson and his colleagues examined the palm-side of *Casineria*'s finger bones, they found furrows that would have held ligaments for bending each digit. This dexterity represents an advance over the Devonian limb design; *Acanthostega* and *Ichthyostega* could only have bent their hands slightly, moving all digits together in an anemic wave.

The capacity to curl each finger separately would have made it easier to negotiate the potential pitfalls of the newly claimed environment, suspects Smithson. "If you're walking over terrain that is rocky or pebbly or has vegetation, then the ability to manipulate your hand in a much more varied way would probably help you get around more easily."

Putting all these features together, *Casineria* seems extremely advanced for its time. "This is quite a sophisticated little critter," comments Coates, who has seen the specimen. "It's a bit like if you are a historian of motor car design and you go back to a 1920s garage and you find, much to your surprise, something that you think would be more at home in a 1950s motor car."

To find out how *Casineria* relates to other creatures, Smithson and his colleagues plugged its anatomical characteristics into a computer program that designs potential evolutionary trees. Their results suggest that *Casineria* did not fit among amphibians but rather sat on the same branch as amniotes—animals with complex eggs. Today, this group includes reptiles, birds, and mammals.

"*Casineria* pulls back the origin of amniote lineages much farther than was previously realized. This creature is the first real evidence of a terrestrial animal that we have, and yet it looks like a close relative of amniotes, if not an amniote itself, which is a bit of a stunner really," says Clack.

Along with its surprises, the tetrapod from Cheese Bay also offers some confirmation for a 30-year-old theory about how amniotes arose.

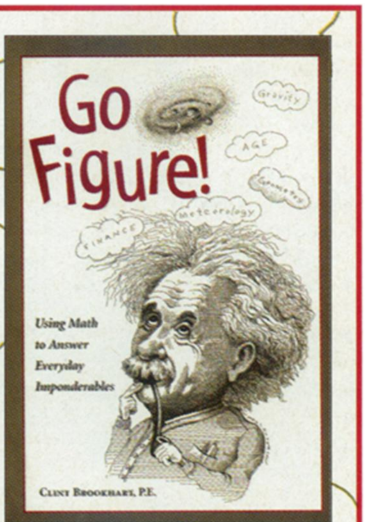
"As soon as I saw the specimen of *Casineria*, I was terribly excited because here was a small form," says paleontologist Robert L. Carroll of McGill University in Montreal. In 1970, Carroll proposed that amniotes evolved from a line of miniature amphibians, much smaller than brutes like *Acanthostega*.

At the heart of Carroll's theory lies the amniote egg, which has a series of membranes not present in the simpler eggs of frogs and salamanders. These extra membranes help transport gases and nutrients around the egg and prevent water from leaking out. The eggs of amphibians make do without such specializations. Because they are all so small, less than half the diameter of a nickel, compounds can easily diffuse throughout the egg.

To solve the puzzle of amniote evolution, Carroll took some clues from the family of small, lungless salamanders known as plethodontids. Unlike many amphibians, most plethodontid salamanders lay their eggs on land and do not pass through a larval stage. Instead, the embryonic salamanders develop directly into an adult body form. The small size of the egg limits how large the adults can eventually grow, he says.

"These modern amphibians that can lay eggs on land and have direct development suggested a model for a transitional animal between the aquatically reproducing amphibians and the terrestrially reproducing early amniotes," says Carroll.

At some point in the Carboniferous period, he hypothesized, a species would have evolved that laid eggs on land, skipped the larval stage of development, and grew straight into small adults. These midgets, he suggests, were the ancestors of amniotes, and *Casineria* looks like the best candidate so far.



"This Cheese Bay animal is very exceptional for fossils of its time in the lower part of the Carboniferous in being small," he says. It's almost small enough to represent a transition between amphibians and amniotes, he suggests.

Over time, these creatures would have evolved eggs with extra membranes, a specialization for life on land that would also have permitted eggs to increase in size. "Once these membranes evolved, then reptiles could get as large as possible," says Carroll.

Initially, though, staying small would have offered some advantages in the world out of water. During the early Carboniferous, there wasn't anything large to eat on land. Vertebrates had not yet evolved the capacity to consume plants, so the only food around consisted of invertebrates—millipedes, centipedes, and the forerunners of insects, says Carroll. Such arthropods would have provided a good diet for a small animal but not a creature the size of *Acanthostega*.

The land shaped its new inhabitants in many other ways. As paleontologists dig deeper into the history of tetrapods, they are growing increasingly convinced that many of the evolutionary changes among these vertebrates have their roots in the new type of ecosystem sprouting on the continents.

During the Devonian period, the first trees evolved and established the earliest forests. This carpet of vegetation held onto soils and kept them from rapidly eroding away, as they had earlier in Earth's history. Shallow swamps appeared, offering a totally new environment for evolution to exploit.

Hand of Casineria *with its five digits (only one finger is complete in photo).*

"What we're looking at is the origin of new types of ecosystems throughout the Devonian. And the origin of tetrapods and of lobe-finned fishes is in part related to that large-scale set of changes, without a doubt," says Neil Shubin of the University of Pennsylvania in Philadelphia.

Limbs with digits would have helped the first aquatic tetrapods negotiate their way through the plant-choked swamps. Only later did these adaptations take on a new role when the early amphibians began crawling out on land, says Shubin.

The types of evolution going on in these swamps led to all sorts of novel arrangements. Last year, Shubin and Edward B. Daeschler of the Academy of Natural Sciences of Philadelphia reported finding a Devonian fish with an array of bones that resemble fingers—a combination not seen in any modern fish. This fish may have used its limbs to creep along the bottom of the swamp as it stalked prey, says Daeschler.

Casineria and its amphibian ancestors would have had good reason to escape these swamps. "It's very clear to me why Devonian tetrapods began to leave. If you look at whom they were living with, most everything is giant. There were 9-feet-long fish, with jaws as big as my arm and pointy teeth as big as my thumb," says Shubin.

With the find of *Casineria*, paleontologists have started to fill in some of the missing evolutionary story between the Devonian swamps and the amniotes of the Carboniferous period. "We've got this gap where we don't have much data. We're beginning to move into that gap—this big blank in the early evolution of tetrapods," says Coates.

Now, researchers must push back their search to the time preceding *Casineria*, when animals were first coming to grips with their new, dry environment. In rocks older than the Cheese Bay specimen, paleontologists will chisel away at the ancient sediments, hammers held tight in a five-fingered grasp that reaches straight through the ages back to the Carboniferous world. ☐